THE COMMUNICATION AND INFORMATION THEORY ASPECTS OF THE NERVOUS SYSTEM

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Paper presented at the
17th Annual Conference in Engineering in Medicine and Biology,
November 18, 1964, Cleveland, Ohio

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(135)

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The quest for a quantitative expression of natural phenomena has lead, in communication theory, to the definition of a quantity of information. The fact that information theory is today applied to several fields other than electrical communications underlines its importance. Information theory fulfills the needs of these various fields for quantitative organization because they present characteristics very similar to those of telecommunication. In the case of the nervous system, for instance, communication is present in the form of impulses (stimuli) conveyed to the central nervous system (CNS) for integration, detection, and computation, or from the CNS to the effectors (muscles, internal glands, etc.).

Having established the link between information theory and the biophysical sciences, we are led to regard the central nervous system as a gigantic information processing device.

There are two ways to consider the phenomenon of nervous communication. First, it may be thought of as a problem in communication itself

in which noise is to be eliminated from the message content through the application of coding and redundancy. Second, nervous communication may be thought of as a problem in data processing where the messages must be stripped of their redundant parts in order to be accommodated in the CNS. These two problems are not contradictory. The first one concerns the retrieval of information from noise; i.e., the coding of information to be transmitted, with a consequent increase in reliability. The second problem concerns the processing of data or the coding of the source information so that redundancy is eliminated. As an analogy, the transmission of English language over a noisy channel can be considered. Before messages are transmitted on the line, all re-dundancies pertaining to the language have to be removed; when this is done, the messages could be coded to combat noise.

The duality of this problem might raise the question: Why does an organism need an elaborate coding scheme if only the pertinent infor-mation is used by its CNS? The answer could lie in the possibility that the data processing is not done only at the CNS but also in the ganglions present along the transmission path. Thus, there would be a great need for efficient coding close to the periphery of the sensorial mechanism. As the information travels up to the CNS, this need might diminish as far as the processing is concerned. But, processing is still needed as far as the noise is concerned since it is reasonable to

assume that the noise increases as the information approaches the CNS. (Noise, as used here, means all unwanted information converging on the CNS at the same time as the wanted information.)

To illustrate this attributed quality of the ganglion, it is only necessary to recall that a constant stimulus, after a certain period of time, does not elicit a response in the neuron. We may postulate that this saving in transmission is accomplished by an accommodation phenomenon in the nervous system.

In order to understand the processes involved in neuron firing, various mathematical models have been evolved such as those by Goldstein,[1] Rosenblith,[2] and Agalides.[3] Goldstein and Rosenblith have represented neuron activity as a resultant of the summation of responses from a whole population of nervous fibers exhibiting the same characteristics. This approach leads to a microscopic view of neural mechanism.[4] Thus, a modified shot noise effect is brought in the picture.

To organize the amount of data available and to extricate from the apparently random nature of the data the statistical parameters necessary for the understanding of the processes at hand, constitute another scientific challenge. We might mention along these lines the contribution already given by spectral analysis to the interpretation of data, as expounded by Wiener[5] and Brazier,[6] where autocorrelation

techniques have helped to detect low frequency phenomena in Electro-Encephalography and to assign different locking frequencies for the various rhythmic activities of the brain (α-rhythm = 10 cps, β-rhythm = 20-25 cps, γ-rhythm = 40-60 cps, δ-rhythm = 1-2 cps, θ-rhythm = 4-7 cps, k (kappa)-rhythm $\approx$ 10 cps).

Throughout the experimental work on the nervous system, both macroscopic and microscopic considerations tend to influence the development of theoretical explanations in nervous transmission in separate, although well-defined, directions. In both cases, we are led to consider the problem of coding and redundancy. These concepts arise when we study the ability of a receiver to detect accurately the nature of the message being sent in the presence of interferring noise. In applying information theory to the nervous system, this problem becomes complicated by two factors not usually encountered in usual telecommunication practice. One, already mentioned above, reflects the difference between macroscopic and microscopic phenomena. The other, which is perhaps more complex involves the presence of both spatial and temporal effects in coding.

It may be said that the presence of both macroscopic and micro-scopic points of view should not necessarily lead to a conflict. This is true in thermodynamics where the former leads to analysis on the basis of ensemble averages, whereas the latter illustrates the dynamics

of individual particles. The study of the nervous system is virtually carried out on this dual basis. However, if we want to analyze communication in the nervous system from the point of view of coding, a conceptual difficulty arises because coding and redundancy do not by necessity belong to either a macroscopic or a microscopic mode. Dr. Brazier,[6] in affect, has suggested that the existence of a multicoding scheme in the nervous system might explain the conveyance of both temporal and spatial information.

The existence of multicoding in the transmission of stimuli to the central nervous system and the macroscopic and microscopic aspects of stimuli transmission are studied. The approaches to the study of these aspects of stimuli transmission are:

1. Microscopic Approach. The transmission of equal stimuli along different individual fibers of the same nervous bundle are studied, and a signal is observed as it travels along the path of the nervous bundle and as it is interpreted by the central nervous system or an integrating organ.

2. Macroscopic Approach. The transmission of equal stimuli along different nervous bundles is studied again with observation of a signal as it travels along an integrating path, and an analysis is made of the signal as it is interpreted by the central nervous system or an integrating organ.

Two types of coding are investigated. In the microscopic approach we attempt to verify that the signal traveling along similar fibers is not necessarily transmitted by similar coding or modulating schemes, but that a multitype of coding is used to provide better noise recording properties. In the macroscopic approach we are concerned with the integration of possible different codes along a complex nervous path, again with a possible gain in information capacity through improved noise contributing properties.

The two approaches have been defined above in broad terms. Note that we have not mentioned the problem of distinguishing between temporal and spatial types of coding. This is because we are only concerned here with the problem of "how" the stimuli are being coded, not with "what" is being coded. This latter problem could only be studied after some definite forms of coding have been established. To find these coding forms we neglect, as a first approximation, another aspect of nervous communication; i.e., the orientation of neural structures.

It is evident that the outlined approaches are of a general nature. As we consider the vast array of neural structures, we find differences in functions.

In the nervous system we are faced with two problems derived from the specific needs of information transmission. One is to find how

to obtain maximum efficiency. The other is how to obtain minimum equivocation. The first problem calls for making maximum use of the capacity of the transmission channels. The second is to find the way to minimize the noise effect, environment, and threshold variation in order to overcome equivocation or misunderstanding.

In the first case, a multiple coding system would be beneficial. Here the term "multiple" means not only the coding in itself but also the system as such. For example, the use of pulse position modulation, pulse duration modulation, and pulse amplitude modulation could be one way to solve the problem of transmitting three different messages over one and the same channel. The effect of noise and the resulting equivocation could be determined by using three or more types of coding systems for one and the same message. Each coded message could then be transmitted over separate channels or over a single channel, depending on the reliability required. See Fig. 1.

A particular noise at a time "t" will not affect all three different modulation systems in the same way and to the same degree. Three types of modulation and two types of noise are shown in Fig. 2. Any one of the noise types will not affect in the same way a pulse duration modulation system, a pulse position modulation system, and a pulse amplitude modulation system.

Figure 3 shows a modulation system with three degrees of freedom.

For a modulation system with three degrees of freedom, the modulated wave can be represented by:
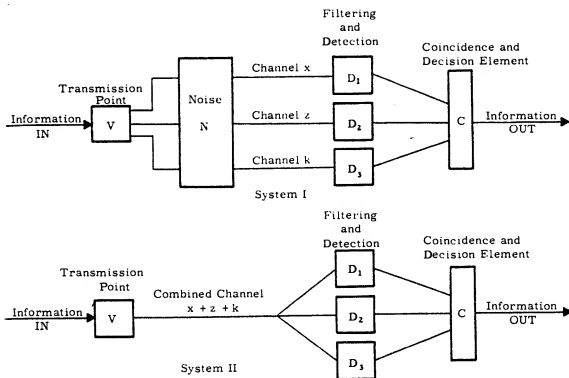
Fig. 1. Multichannel multicoding and unichannel-multicoding transmission and reception systems.
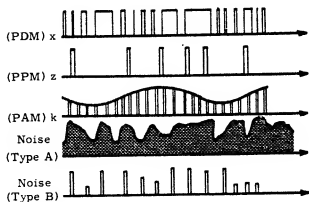

Fig. 2. PDM, PPM, PAM, and two types of noise transmitted simultaneously.
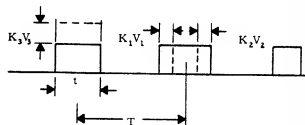
Fig. 3. Pulse modulation with three degrees of freedom (applying PDM, PPM, and PAM at the same time).

$$M(t) = \frac{t_0}{T} + \frac{t_0 K_3 V_3 (T_n)}{T} + \frac{2A_n}{T}$$

$$+ \frac{2A_n K_3 V_3 (T_n)}{T} + \sum_{m=1}^{\infty} \frac{2}{m\pi} [1 + K_3 V_3 (T_n)]$$

$$\sin m\omega_c [\frac{t_0}{2} + A_n] \cos (m\omega_c t - m\omega_c B_n),$$

where

$$A_n = \frac{K_1 V_1 (T_n) - K_2 V_2 (T_n)}{2}$$

$$B_n = \frac{K_1 V_1 (T_n) + K_2 V_2 (T_n)}{2}$$

$$A_n + B_n = K_1 V_1 (T_n)$$

$$B_n - A_n = K_2 V_2 (T_n)$$

$$a_0(n) = \frac{1}{T} \int_c^d [1 + K_3 V_3 (T_n)] \, dt$$

$$= \frac{1 + K_3 V_3 (T_n)}{T} t_0 + 2A_n$$

$$a_m(n) = \frac{2 [1 + K_3 V_3 (T_n)]}{m\pi}$$

$$\sin m\omega_c [\frac{t_0}{2} + A_n] \cos m\omega_c B_n$$

$$b_m(n) = \frac{2 [1 + K_3 V_3 (T_n)]}{m\pi}$$

$$\sin \omega_c B_n \sin m\omega_c [\frac{t_0}{2} + A_n].$$

The unmodulated pulses are ideal rectangular pulses with time duration t_0, amplitude unity, and repetition period T. The leading edge is modulated with modulation factor K_1 and the trailing edge with a modulation factor K_2. $V_1(t)$ and $V_2(t)$ are independent modulating waves; $n = 0, \pm 1, \pm 2$; and T_{n_1} and T_{n_2} denote the respective times in the n th period that $V_1(t)$ and $V_2(t)$ are sampled. We may assume that $T_{n_1} = T_{n_2} = T_n$. With uniform sampling, $T_{n_1}, T_{n_2}, \cdots T_{n_n}$ can be replaced by T_n. The terms $a_m(n)$ and $b_m(n)$ are constants over any one period T_1 but may vary from period to period. Also $\omega_c = 2\pi/T$. Finally, K_3 is a modulation factor applied to the amplitude of the pulse.

A modulation form prevalent in living organisms is Pulse Repetition Rate Modulation (PRRM). This type of modulation is a digital equivalent of the frequency modulation of an analog signal. A form of pulse repetition rate modulation is found in the spinal cord. In the skin receptors, transmission of stimuli seems to occur in the form of a pulse position modulation system. Graded signals in the nervous system seem to belong to an amplitude modulation system.

We can now state that in complex living organism like vertebrates there are many modulation systems used for transmitting information. In addition there are different types of coding. The name of multi-dimensional coding could be applied to the form in which different coded signals are transmitted over one and the same channel at the same time.

Brazier mentioned the multitude of codes existing in the nervous system at the 1960 Moscow Conference on Higher Nervous Activity. It can be shown that the multiple coding system represents an economy in the transmission channels in the case of different stimuli. On the other hand, if the same stimulus is transmitted by a multi-channel multi-coding system, there is a definite advantage as compared with the transmission of the stimulus by a single coding system. This is true regardless of how good a single coding system can be because it can be one of the multiple coding systems.

To ascertain the existence of different types of codes, we investigated the response of different stimuli on the skin sensory receptors. The first receptor to be studied was the Pacinian Corpuscle (Fig. 4). Agalides compared the elicited responses to mechanical and acoustic stimuli.[7] The
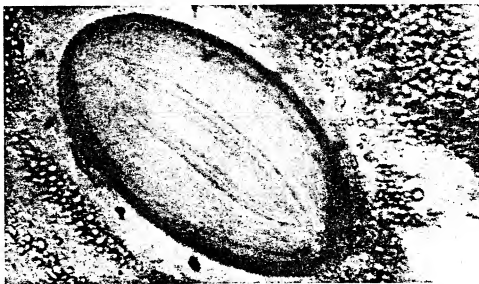

Fig. 4. Photomicrograph of a Pacinian Corpuscle, 40X. (Nikon Interference Phase Microscope, Nikon Microflex Camera, Tri-Pan-X Kodak Film; exposure time, 0.5 sec.)

difference between the form, amplitude and latency involved for each response
was shown (Figs. 5, 6, 7). The power and frequency curves of the trans-
ducers were plotted. There is a definite difference between the response
of the same receptor to mechanical and to acoustical stimuli. This was an
investigation in vitro. If the coding in the nervous system in vivo should be
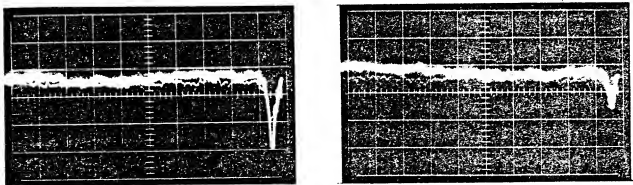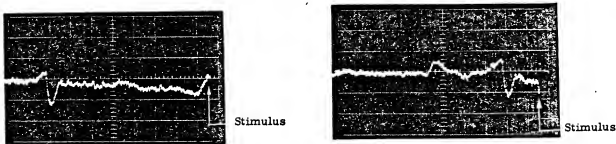studied, then either gross recording electrodes or microelectrodes can be used.

Fig. 5. Impulses from a Pacinian Corpuscle; stimulus, mechanical
pressure; vertical scale, 20 μv/division (large scale); horizontal
scale, 10 ms/division (large scale).

Figs. 6 and 7. Effect of acoustical wave pressure on Pacinian Corpuscle.
B and K heterodyne oscillator and amplifier; 70 cps,
keyed; 100 v rms on the piezo-electric acoustic transducer,
one electrode grounded. Recorded between the Pacinian
Corpuscle and first node of Ranvier and the axon of the
sensory receptor at a distance of 7 mm from the corpuscle.
Vertical scale, 10 μv/division (large scale); horizontal
scale, 1 ms/division (large scale).

The damage done to the surrounding cells by inserting electrodes into the nervous system cannot be overlooked. Another approach for studying in vivo coding processes in living organisms is via an investigation of the electrical activity of electric fishes.

Figure 8 shows some representatives of gymnotid fishes from tropical and equatorial South America and mormyrid fishes from tropical and equatorial Africa. Some of the fishes having electric organs use them for offensive and defensive purposes. These are strong electric fishes whose discharge can paralize prey or at least scare away enemies. Torpedo Nobiliana, a marine electric fish, can discharge electric pulses of some 220 volts. The short-circuit current of an adult Torpedo can reach 50 amperes. The output capabilities of Electrophorus Electricus, the Electric Eel, (Fig. 9), a fresh-water electric fish, were studied. Voltage discharges of over 600 volts were measured. The maximum current at 10 ohms load resistance was close to one ampere. The pulse peak power was around 100 watts.

There are other electric fishes, called weak electric fishes, which use electric coded impulses for navigation and communication purposes. Pulse shape and pulse duration are very different depending on species.

The electric eel has three electric organs, each of which performs different functions. One is called the main electric organ and
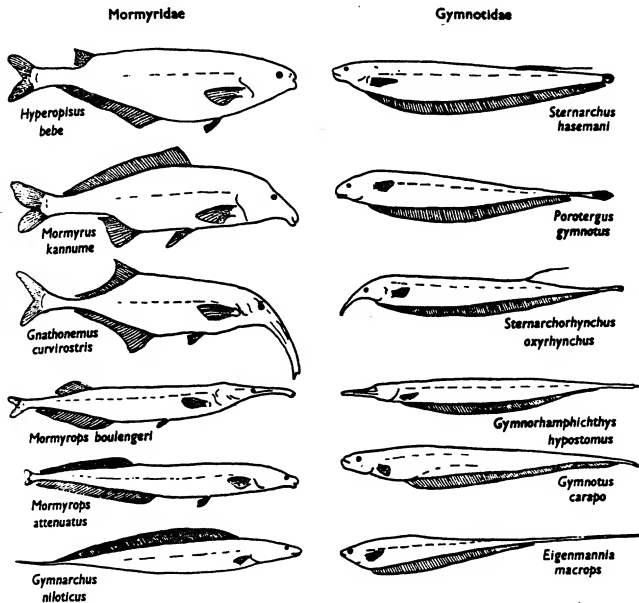
Figure 8. Representative types of the Mormyridae and Gymnotidae.
The convergent evolution between these unrelated families
is expressed in terms of their electric discharges, reduction
of the tail fin, propulsion through an elongated unpaired fin,
development of long snouts, and several other features.

Fig. 9. Electrophorus Electricus (electric eel).

produces high voltage pulses used for stunning purposes. Another electric
organ, called the organ of Hunter, is used for communication and navi-
gation purposes. A third electric organ, called the organ of Sachs, is
thought to have an auxiliary function and its electric discharge is much
weaker than that of the main electric organ.

By studying the form and shape of the coded impulses, we can dis-
tinguish a large variety of coding systems (Figs. 10, 11). Gymnarchus
Niloticus, an electric fish from equatorial and tropical Africa, studied
in detail by Lissman and Machin[8], is one of the most sensitive electric
fishes. It can sense any disturbance of the surrounding water produced
by objects. It can distinguish between electric conductors and micro-
conductors. Charges of the electric field of 0.03 μv/cm produced by
direct currents can be detected by Gymnarchus Niloticus. Its receptor
system operates in the second derivative mode. The change in current
in the electroreceptors was calculated to about 0.003 $\mu\mu$a for 1 ms pulses
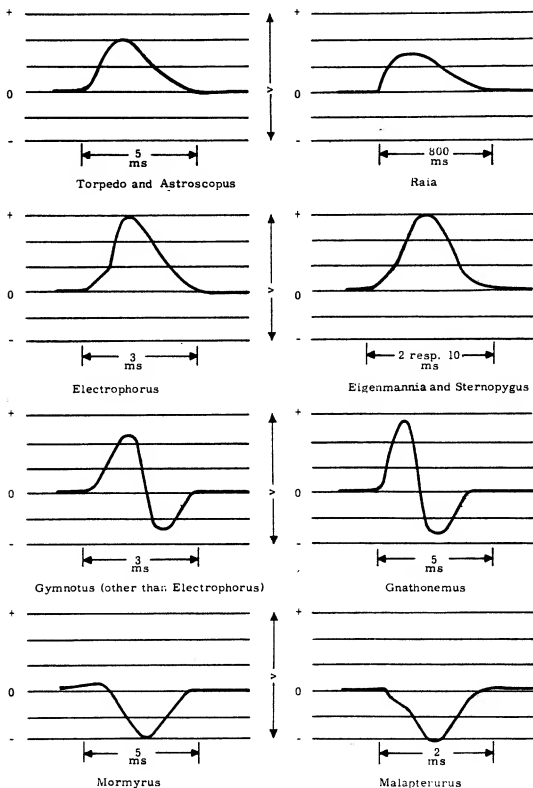at a frequency of 300 cps.

Fig. 10. Pulse shape and pulse duration of the discharges of some species of electric and magnetic sensitive fish. (After H. Grundfest, 1952)
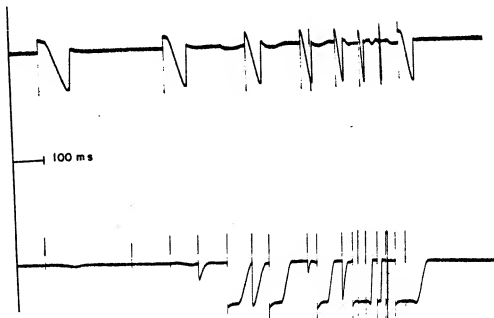
Fig. 11. Cross communication between two electric eels in two separate
aquaria; optical galvanometer recorder, dc to 10 kc frequency
range, speed 76 mm per second.

Gnathonemus Petersii (Figs. 12, 13), an African electric Mormyrid,
utilizes a pulse position plus pulse amplitude modulation. The slope of the
pulse is less than 50 μsec, and the entire pulse duration is 250 μsec.

Sternarchus Albifrons (Figs. 14, 15, 16), a South American Ster-
narchid, utilizes a permuted phase plus an amplitude modulation coding
system.

Electrophorus Electricus utilizes a very complicated coding method
in conjunction with a modulation system with three degrees of freedom.

It was verified that the fish can decode the electric signals emitted by
other fish of the same species. The experiment proving this fact was
reported at the 1964 Rochester Conference on Data Acquisition and Processing
in Biology and Medicine.[9]

By studying the types of coding used by fishes for perhaps twenty or thirty million years, we can once more observe that evolution has solved biochemical, electrical, and mechanical problems of energy transformation by always finding the way to utilize minimum energy combined with excellent efficiency. In the case reported on here, evolution found the way to extract signals from noise with little power utilization. The study of the natural phenomena and of living organisms still can provide the scientist with new clues and means to further the general progress of science.

Acknowledgement

I wish to express my appreciation for the support offered by the Air Force Office of Scientific Research, Information System Directorate; the Office of Naval Research, Biology Branch; and General Dynamics/Electronics. In particular I wish to thank Dr. H. C. Nedderman, Director of Research for GD/E, for his managerial assistance. Mr. Bernardini was responsible for the excellent microsurgery required to dissect the Pacinian Corpuscle, the electric organs of electric fishes, and their brains. Mr. R. Zinsmeister set up the electric equipment and skillfully recorded the electrical activity of electric fishes and that of the skin sensory receptors. Finally I would like to thank Mr. R. Doughty for his help in editing this article.
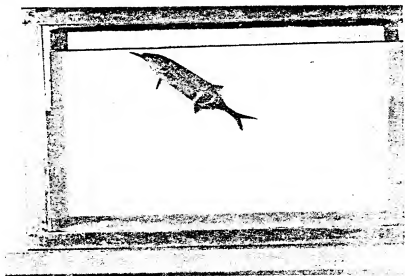
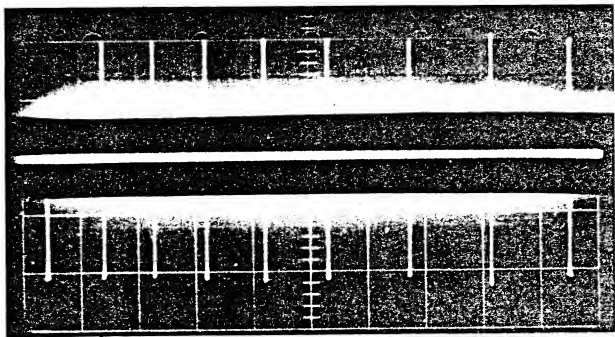Fig. 12.   Gnathonemus Petersii
            (African electric fish).

Fig. 13.   Electrical signals emitted by Gnathonemus Petersii.
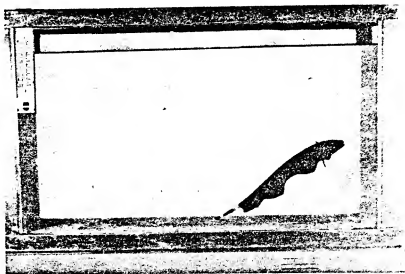   Scales: vertical, 50 mv/div; horizontal, 50 ms/div.

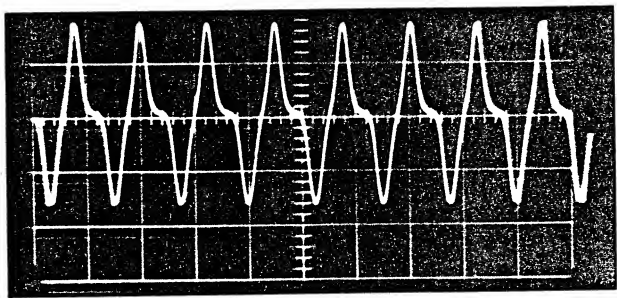Fig. 14. Sternarchus Albifrons
(South American electric fish).

Fig. 15. Electrical signals emitted by Sternarchus Albifrons.
Scales: vertical, 2 mv/div; horizontal, 1 ms/div.

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Recording made with two stainless steel electrodes, 7 inches long, placed in the water tank.
Recorder: Midwestern Optical Recorder.
Amplifiers: (1) Tektronix and (2) specially constructed units.
Date of recording: 2 February 1963   Time: 2:00 PM   Recorder speed: 60 ips
Voltage at electrode: 1 mv (equals 1.6-inch deflection on recording paper).
Voltage at output of second amplifier: 1.1 v (equals 1-inch deflection on recording paper).

Fig. 16. Recording of the electrical activity of Sternarchus Albifrons.

BIBLIOGRAPHY

1. Goldstein, M. H. , Jr., "A Statistical Model for Interpreting Neuroelectric Responses," Information and Control, 3, pp. 1-17 (1960).

2. Rosenblith, W. A., editor, "Sensory Communication," MIT Press and John Wiley and Sons, Inc., p. 196 (1961).

3. Agalides, E., "The Mathematical Model of the Neuron," Rochester Conference on Data Acquisition and Data Processing in Medicine and Biology, Pergamon Press 1962.

4. Adolph, A. R., "Sensory Neurology and Analog" Technical Document LMSD 49752, Lockheed Aircraft Corp. (June 1959).

5. Wiener, N., "Cybernetics," or "Control and Communication in the Animal and the Machine," MIT Press and John Wiley and Sons, Inc., Chapt. 10 (1961).

6. Brazier, M. A. B., "Long-persisting Electrical Traces in the Brain of Man and Their Possible Relationship to Higher Nervous Activity," Moscow Symposium on Higher Nervous Sensitivity, 1960.

7. Agalides, E., "The Effect of Acoustical Waves on the Pacinian Corpuscle," Transaction of the New York Academy of Sciences, Vol. , No. , April 1964.

8. Lissman, H. W. and K. E. Machin, "The Mechanism of Object Location in Gymnarchus Niloticus and similar Fishes," J. Exper. Biology, 35, 451 (1958).

9. Agalides, E., J. Bernardini, and R. Zinsmeister, "Information Processing by Electric Fishes," Proceedings of the 1964 Rochester Conference on Data Acquisition and Processing in Medicine and Biology, ed., by K. Enslein, in press: Pergamon Press, London and New York.